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ARTICLE

Temporal and Spatial Dynamics of the Lionfish Invasion in the Eastern Gulf of Mexico: Perspectives from a Broadscale Trawl Survey

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Abstract
The recent introduction of invasive Indo-Pacific lionfish species (Red Lionfish *Pterois volitans* and Devil Firefish *P. miles*, hereafter collectively referred to as lionfish) into the western Atlantic Ocean has been extensively documented in both the scientific literature and the media. Nevertheless, much of the information synthesized has been obtained via diver-based surveys and there is likely a depth-related bias to the understanding of the temporal and spatial dynamics of the lionfish invasion. Accordingly, we examined data from a broadscale fisheries-independent trawl survey of bare substrates and low-relief habitats that was initiated in 2008 in the eastern Gulf of Mexico. Lionfish were first observed in the survey in 2010, when two individuals were collected off southwestern Florida. The distribution of lionfish continued to expand northward through the Florida panhandle in 2011 and 2012, when 40 and 29 lionfish were collected, respectively. A dramatic increase in the abundance (391 individuals) and distribution of lionfish occurred in 2013. Evidence from this survey suggests that lionfish first colonized deeper (>30 m) low-relief habitats before populations expanded into shallower waters. The prevalence of lionfish on primarily nonreef habitats at depths beyond those frequented by recreational divers will likely have important implications for efforts to control or eradicate lionfish populations in the region. Moving forward, information from long-term, multispecies surveys such as this will continue to provide valuable insight into the spatial and temporal dynamics of the lionfish invasion and allow us to assess long-term ecological consequences of increasing lionfish abundances.

Range expansion into the western Atlantic Ocean by two invasive Indo-Pacific lionfish species, the Red Lionfish *Pterois volitans* and the Devil Firefish *P. miles* (hereafter collectively referred to as lionfish), has progressed at an unprecedented rate. Lionfish were first reported off southeastern Florida in the mid-1980s; the distribution of reported lionfish sightings remained localized through 1999, after which they rapidly expanded their range (Schofield 2009, 2010; Johnston and Purkis 2011). From 2000 to 2006, lionfish expanded northward along the eastern U.S. coastline, to Bermuda, and subsequently to the Bahamas.

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Since 2007, lionfish have spread throughout the Caribbean, reaching the Florida Keys in 2009 (Ruttenberg et al. 2012) and the Gulf of Mexico in 2010 (Schofield 2010; Fogg et al. 2013). Often strongly associated with reef habitats (Schultz 1986; Biggs and Olden 2011; Claydon et al. 2012), lionfish in the western Atlantic Ocean have been found to occupy mangrove (Barbour et al. 2010; Claydon et al. 2012; Pimiento et al. 2015), seagrass (Biggs and Olden 2011; Claydon et al. 2012), and lower riverine habitats (Jud and Layman 2012) as well.

Although the invasion and subsequent expansion of lionfish populations throughout the western Atlantic Ocean have been generally well documented (Côté et al. 2013), most studies have relied heavily on data collected by recreational or scientific divers (Schofield 2009, 2010; Ruttenberg et al. 2012; Scyphers et al., in press). As a result, the understanding of the dynamics of the lionfish invasion in waters deeper than those routinely sampled by diver-based surveys (~35 m) is somewhat restricted. Several studies have documented lionfish at depths as great as 100 m (Meister et al. 2005; Whitfield et al. 2007; Lesser and Slattery 2011; Nuttall et al. 2014), where water temperatures are well within the thermal tolerances of the species (Kimball et al. 2004). The effectiveness of diver-based control efforts directed at shallow-water lionfish populations may be undermined by rapidly increasing lionfish populations at greater depths. A more quantitative examination of depth-related lionfish population dynamics is essential for informing population control strategies and quantifying ecological impacts. Accordingly, we analyzed data from a broad-scale, fisheries-independent trawl survey to (1) characterize the range expansion of lionfish in the eastern Gulf of Mexico from 2010 through 2013 and (2) assess depth-associated patterns in lionfish abundance, frequency of occurrence, and size.

METHODS

Study area.—Our analyses focused on data collected in the eastern Gulf of Mexico, from the Dry Tortugas north to the Florida–Alabama border, at depths from 4 to 104 m. Sediment composition in the eastern Gulf of Mexico is dominated by quartz-rich sand on the inner shelf, mollusk-rich sand over a broad area of the middle shelf, and sand rich in coralline algae on the outer shelf (Randazzo and Jones 1997). Although trawlable, nonreef bottom habitat is abundant, most of the natural hard-bottom habitat in the Gulf of Mexico is found off of Florida and the Yucatan Peninsula, with patches of coral and sponge habitat occurring extensively along the West Florida Shelf (WFS) (Briggs 1958; McEachran and Fechhelm 1998). Much of the multibillion-dollar fishing industry in the eastern Gulf of Mexico is derived from species associated with these hard-bottom habitats.

Field methods.—Data were collected as part of the recent Florida expansion of the Southeast Area Monitoring and Assessment Program's (SEAMAP) annual summer groundfish trawl survey. This survey (Eldridge 1988) employs a stratified-random sampling design in which annual sampling effort is proportionally allocated among depth and geographic strata. Initiated in the early 1980s, the SEAMAP groundfish trawl survey originally extended from the Mississippi–Alabama border westward to the Mexico border, encompassing National Marine Fisheries Service (NMFS) statistical reporting zones 11–21. In 2008 and 2009, exploratory summer surveys were conducted from Tampa Bay to Alabama (NMFS zones 5–10) to investigate the feasibility of expanding the SEAMAP groundfish survey into the eastern Gulf of Mexico; this survey was expanded to encompass NMFS zones 2–10 in 2010 (Figure 1). All samples were collected during June and July using a standard 12.8-m SEAMAP shrimp trawl towed at a speed of 3 knots, and tow duration was generally 30 min (bottom sampling area = approximately 1.03 ha/tow). Trawls were typically towed over bare substrates or low-relief habitats to minimize damage to sensitive bottom communities. All lionfish collected were enumerated and measured to the nearest millimeter standard length (SL), and pertinent site information was recorded, including location and water depth. Additional survey details can be found in Rester (2011).

Analytical methods.—To visually explore the patterns of lionfish expansion in the eastern Gulf of Mexico, the locations where trawl sampling was conducted and those where lionfish were collected were plotted annually in a GIS, with symbol size being proportional to the number of lionfish collected. No lionfish were collected in the 2008 or 2009 trawl surveys, so those data were not included in subsequent analyses. For data collected between 2010 and 2013, summary statistics were calculated of the annual trawl sampling effort, frequency of lionfish occurrence (percentage of annual trawl samples that contained at least one lionfish), total number of lionfish collected, and mean number of lionfish collected per trawl. Annual length frequency distributions were also constructed, and a series of Kolmogorov–Smirnov two-sample tests, using the Bonferroni correction for multiple pairwise comparisons ($\alpha = 0.05/3$ or 0.017), were used to compare length frequency distributions between all years excluding 2010 (SAS Institute 2006; Sokal and Rohlf 2012). For 2013 data only, the mean number of lionfish per haul and mean size of lionfish collected (mm SL) were compared among depth bins using one-way analysis of variance (ANOVA) and the Tukey–Kramer adjustment for pairwise comparisons (SAS Institute 2006); depth intervals were chosen to divide the data into six depth quantiles. The frequency of occurrence data, in terms of overall sampling effort as well as samples containing lionfish, were summarized for 10-m depth bins and analyzed via habitat suitability analysis (Baltz 1990) to explore nonlinear patterns of habitat selection along the gradient of depths sampled.

RESULTS

Lionfish were first collected in survey trawls in 2010 (Figure 2; Table 1), when two individuals were captured off

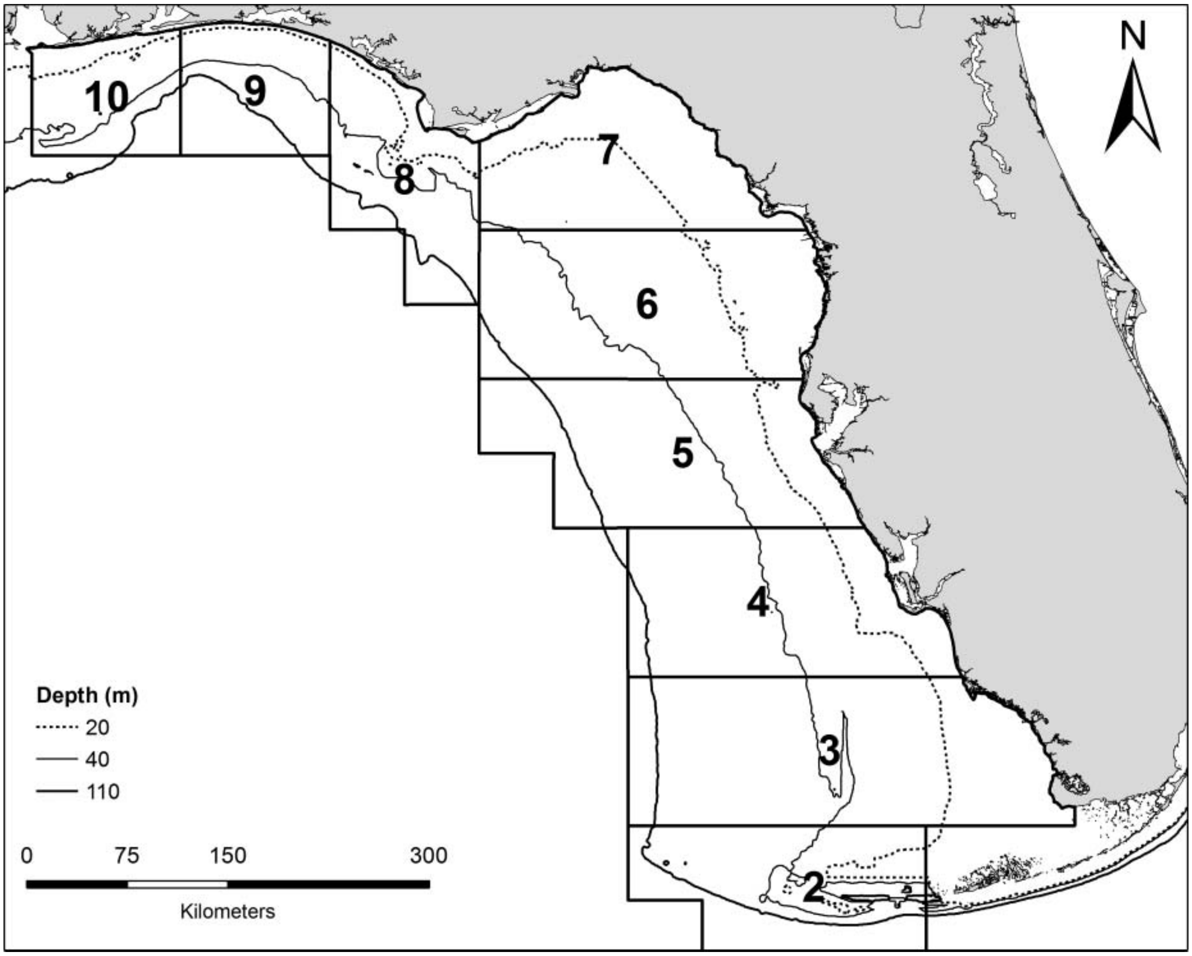

FIGURE 1. Spatial extent of the Southeast Area Monitoring and Assessment Program (SEAMAP) trawl survey in the eastern Gulf of Mexico. Annual sampling effort is allocated proportionally among statistical reporting zones (2–10) based on the total area of the seafloor from 4 to 110 m.

Florida's southwest coast in depths of approximately 45 m. In 2011 and 2012, lionfish were more abundant ($N = 40$ and $N = 29$, respectively) and catches expanded northward into waters off the Florida panhandle. This expansion first occurred primarily in deeper waters but extended inshore after 2012. A dramatic increase in abundance occurred in 2013 ($N = 391$ lionfish). That year, lionfish were collected in 40% of all trawl samples and at a mean rate of 2.57 individuals/haul (SE, 0.44).

The size of lionfish captured in trawls has increased since the initial invasion into the eastern Gulf of Mexico (Table 1; Figure 3); at $\alpha = 0.017$ for each pairwise test, length frequency distributions did not differ between 2011 and 2012 ($P_{KS} = 0.03$) but did differ between 2011 and 2013 ($P_{KS} < 0.01$), as well as between 2012 and 2013 ($P_{KS} < 0.01$). In 2010, both individuals collected were less than 100 mm SL, but maximum size had exceeded 300 mm by 2012 and 400 mm by 2013. In 2013, both mean lionfish abundance ($F = 9.18$; $P < 0.01$) and size ($F = 3.60$; $P < 0.01$) differed significantly among the depths sampled (Figure 4). The mean abundance of lionfish was significantly greater in depths from 49 to 67 m than it was in depths less than 35 m, whereas the mean size of lionfish was significantly greater in depths from 49 to 67 m than it was in depths from 27 to 35 m. Overall, lionfish exhibited the highest suitability at depths from 30 to 80 m (Figure 5); no lionfish were collected in waters shallower than 20 m in any year of the survey.

DISCUSSION

This study in the eastern Gulf of Mexico provides the first quantitative description of the lionfish expansion that considers predominantly nonreef habitats and depths beyond those examined in most prior studies. Although the lionfish invasion has been well documented in general, most available literature has emphasized the colonization of shallow habitats (e.g., reefs or various estuarine habitats) at depths accessible to divers. However, lionfish have been observed in waters as deep as 100 m in the western Atlantic Ocean (Meister et al. 2005; Whitfield et al. 2007; Lesser and Slattery 2011) and

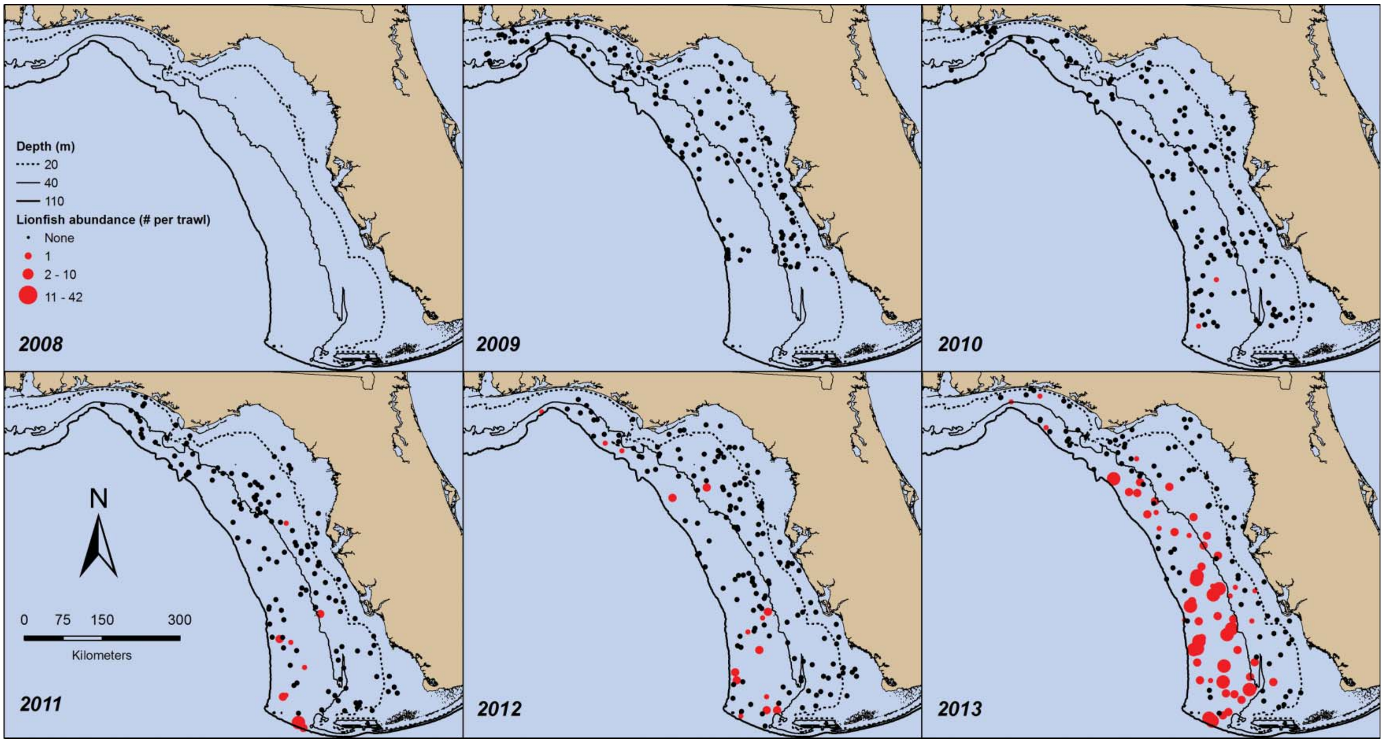

FIGURE 2. Spatial distribution of lionfish collected during the annual (2008–2013) summer SEAMAP trawl surveys in the eastern Gulf of Mexico. The black circles represent the locations where trawl samples were collected and no lionfish were captured. The red circles represent the locations where lionfish were collected, and the size of each red circle represents the relative number of lionfish collected within each set.

northwestern Gulf of Mexico (Nuttall et al. 2014). Using a stratified-random sampling design across depths to 104 m, we detected the initial expansion into the southeastern Gulf in 2010, which coincides well with the first reports from the lower Florida Keys (Schofield 2010). However, diver-based sightings of lionfish during late 2010 in shallower waters off the Florida panhandle and central western coast (USGS 2014) suggest there were likely multiple and simultaneous expansion pathways into the eastern Gulf of Mexico. Because the SEAMAP trawl survey did not include the extreme southeastern portion of the gulf before 2010, we cannot confirm or refute the notion that introduction into the gulf was possible as early as 2008, an idea based on the projected age at length (e.g., Barbour et al. 2011) of a single large specimen collected in 2012 (Fogg et al. 2013). Nevertheless, the first reported lionfish sighting from the Dry Tortugas did not occur until late 2009 (Schofield 2010), so it is doubtful that lionfish would have been collected even if trawl effort had been allocated to the region during that period.

The results from this study indicate that in the eastern Gulf of Mexico lionfish likely first settled in deeper habitats along the WFS. Central America is identified as the probable source of lionfish in the gulf (Johnston and Purkis 2011), and deeper WFS habitats would have been the first ones encountered by larvae transported by prevailing currents (e.g., the Yucatan and Loop currents). The incursion of the Loop Current into the Gulf of Mexico varies during the year, typically attaining its most northerly intrusion during the summer (Sturges and Evans 1983). With Loop Current surface velocities exceeding 60 cm/s in early summer 2010 (Hamilton et al. 2011) and the mean settlement age for planktonic Red Lionfish larvae estimated at 26.5 d (Ahrenholz and Morris 2010), lionfish larvae from the Yucatan could have been transported more than 1,300 km before settlement, placing them along the eastern wall of the Loop Current and in proximity to the WFS. Drift-buoy trajectories recorded during that period also identified cyclonic eddy flows along the eastern Loop Current wall that forced a northward counterflow along the west Florida slope (Hamilton et al. 2011). The overall increase in size from 2010 to 2012, combined with distribution records, provides evidence of a general northward expansion within deeper waters prior to the population expansion inshore. Lionfish become reproductively active within their first year (Morris and Whitfield 2009), and a growing pool of larvae originating from both early colonizers to the WFS and from exponentially growing upstream populations likely facilitated a secondary and more radial population expansion across WFS habitats. Four years after the initial invasion onto the WFS, lionfish densities remain highest in depths of 40–80 m, similar to recent observations in mesophotic depths of the northwestern Gulf of Mexico (80–90 m; Nuttall et al. 2014). In their native range, lionfish are collected most often in shallower waters

TABLE 1. Annual sampling effort and overall catch data for lionfish collected during the summer SEAMAP trawl survey in the eastern Gulf of Mexico.

Year	Total number of samples	Mean (range) sampling depth (m)	Number (and percent) of samples containing lionfish	Total number of lionfish collected	Mean ± SE lionfish per haul	Mean (range) standard length (mm)
2010	161	39 (7–100)	2 (1.2%)	2	0.01 ± 0.01	91 (85–97)
2011	143	38 (4–97)	9 (6.3%)	40	0.28 ± 0.14	174 (129–251)
2012	162	37 (9–101)	16 (9.9%)	29	0.18 ± 0.05	172 (70–337)
2013	152	41 (5–104)	61 (40.1%)	391	2.57 ± 0.44	208 (62–404)

(Kulbicki et al. 2012); as populations continue to increase in abundance, we expect lionfish density in shallower waters to increase.

Although gonads were not analyzed, a significant proportion of lionfish collected in this study were large enough to be reproductively active (Morris and Whitfield 2009), so nonreef habitats in deeper waters may be an important source of lionfish larvae. In general, the SEAMAP trawl survey is restricted to bare substrates or low-relief habitats, but because very little high-resolution habitat information is available for much of the study area, some samples were collected over or near live bottom (sponges, gorgonians, etc.) and higher-relief reef structure. Lionfish use a variety of marine substrates in both their native and nonnative ranges, but they are most commonly associated with structured habitats such as reefs, mangrove swamps, and artificial structure (Barbour et al. 2010; Kulbicki et al. 2012; Schofield et al. 2014). Several studies have documented, to some extent, ontogenetic shifts in habitat affinity. In studies from Roatán, Honduras (Biggs and Olden 2011), and the Turks and Caicos islands (Claydon et al. 2012), smaller lionfish tended to occupy seagrass habitats, whereas mature individuals were associated with structured reef environments. Consequently, the lionfish abundance and length data collected from low-relief habitats in the eastern Gulf of Mexico may not represent the portion of the population associated with more structured habitats. Furthermore, the size distribution of our catch is strongly influenced by the trawl sampling gear and small postsettlement individuals were not collected in our surveys. Nevertheless, these data provide a conservative and quantitative estimate of the rapid population growth in the eastern Gulf of Mexico. To fully describe the dynamics of lionfish populations in these deeper environments will require data from sampling methods complementary to this trawl survey, such as traps or underwater cameras, that can effectively quantify biota in reef or live-bottom habitats (Bacheler et al. 2013; Dahl and Patterson 2014; Nuttall et al. 2014).

The widespread establishment of lionfish populations in the eastern Gulf of Mexico beyond depths accessible to divers

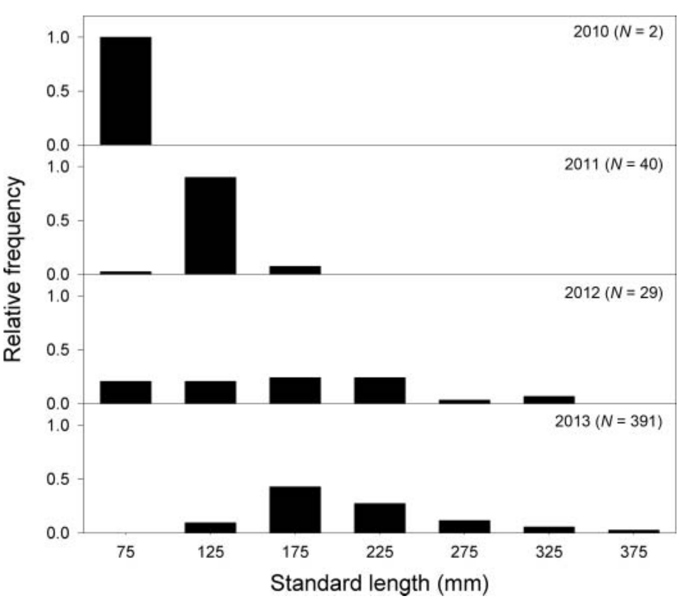

FIGURE 3. Annual length frequency distribution of lionfish collected during the summer SEAMAP trawl surveys in the eastern Gulf of Mexico (2008–2013; no lionfish were collected in 2008 or 2009). Values along the *x*-axis represent midpoints of 50-mm size-class bins.

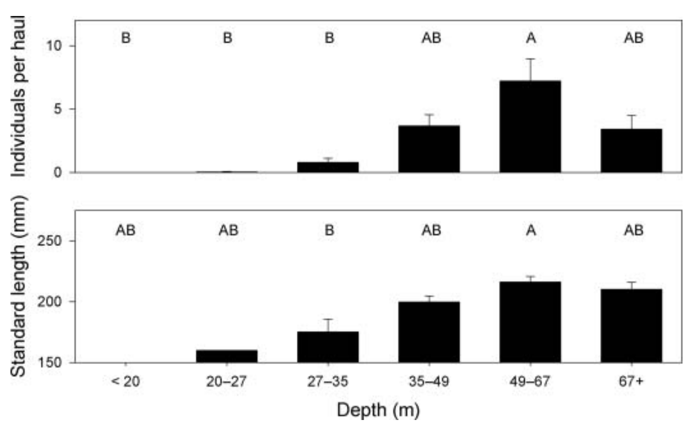

FIGURE 4. By depth, the average number of lionfish per trawl (upper panel) and the average standard length of lionfish (lower panel) collected during the summer 2013 SEAMAP trawl survey in the eastern Gulf of Mexico (error bars indicate SE). Mean values were compared by ANOVA, and the letters above each bar represent groupings as determined via pairwise tests between depth quantiles (means with at least one letter in common are not significantly different).

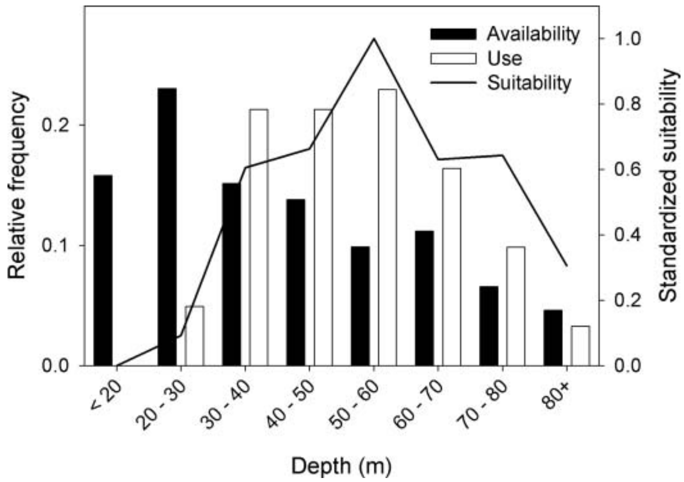

FIGURE 5. Depth-associated habitat suitability for lionfish collected during the summer 2013 SEAMAP trawl survey in the eastern Gulf of Mexico. The black bars represent the relative frequency of depth sampled, the white bars represent the relative frequency of depths within which lionfish were captured, and the black line represents the calculated habitat suitability.

likely has important implications for control strategies and fisheries management. There is little evidence that lionfish populations are vulnerable to biological controls such as predation (Hackerott et al. 2013), and there is very limited information on their susceptibility to parasitism (Ruiz-Carus et al. 2006; Bullard et al. 2011) or disease in nature. A single lionfish, believed to have been released from an aquarium, was collected in 2006 in association with a red tide bloom near Pinellas County, Florida (Schofield 2010), and frequent episodic red tide events in the eastern gulf may provide some level of control in shallow coastal habitats as populations expand into nearshore regions. At present, removal of lionfish by divers is probably the most common method of control, but this method is generally applicable to waters shallower than ~35 m. Lionfish are rarely caught in hook-and-line fisheries but have been reported as incidental catches in some deepwater fisheries (Akins 2012) and are frequent bycatch in commercial trap fisheries (National Marine Fisheries Service, Southeast Fisheries Science Center, Trip Interview Program, personal communication). Recently developed models predict that containment of lionfish populations will prove very difficult if portions of the adult populations remain unexploitable (Arias-González et al. 2011). Accordingly, the development of directed trap fisheries for lionfish may offer alternatives to removal by divers in these deeper habitats. In deeper waters, many ecologically and economically important reef fishes utilize habitats that overlap with those of lionfish, and species such as Red Grouper *Epinephelus morio*, Vermilion Snapper *Rhomboplites aurorubens*, Gray Snapper *Lutjanus griseus*, and Lane Snapper *L. synagris* were often caught in conjunction with lionfish in our survey trawls. The ecological effect of proliferating lionfish populations on these economically important native species and their prey base is unknown, but recent investigations conducted in shallower waters of the Bahamas document the potential for adverse impacts (Albins and Hixon 2013) on native reef fish recruitment (Albins and Hixon 2008) and prey species' biomass (Côté and Maljkovic 2010; Green et al. 2012). At mesophotic depths, declines in coral reef herbivores caused by lionfish predation or avoidance of lionfish resulted in a phase shift to algae-dominated communities (Lesser and Slattery 2011).

To date, our data suggest that the lionfish expansion in the eastern Gulf of Mexico is still in progress, yet it is unclear how long it will continue. Results from ongoing trawl surveys in the eastern Gulf of Mexico should allow us to document when lionfish abundances eventually level off. Further, this survey, which began before the invasion, should allow us to monitor and assess long-term ecological consequences of increasing lionfish abundances in the eastern Gulf of Mexico.

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